The Veliger 29(3):256–259 (January 2, 1987)

THE VELIGER

Spawning and Hatching of *Cypraecassis testiculus* Linnaeus, 1758 (Tonnacea: Cassidae)

by

ROGER N. HUGHES AND HELEN P. I. HUGHES

School of Animal Biology, University College of North Wales, Bangor, Gwynedd, LL57 2UW, U.K.

Abstract. *Cypraecassis testiculus* spawn in the shallow water of reef flats of Barbados during the spring. Egg capsules are deposited in double, arc-shaped rows on the undersides of stones. Each cylindrical capsule contains some 1500 eggs of about 150 μm in diameter when newly laid. A female produces about 800 capsules and so has a fecundity of about 1.2 million eggs per spawning. The eggs lie as a single layer between the capsular wall and a central jelly matrix. During early development, veligers appear to consume this central "albumen." Prior to emergence, veligers jettison the pair of dark red larval kidneys. Veligers emerge from the capsule after 13–17 days, depending on temperature, and enter a planktotrophic phase of unknown duration, but during which the protoconch grows 1–2 additional whorls.

INTRODUCTION

Cypraecassis testiculus, family Cassidae, superfamily Tonnacea, inhabits rocky reef-flats throughout the Caribbean Sea, where it feeds on echinoids (HUGHES & HUGHES, 1981). In common with other cassids, *C. testiculus* deposits egg capsules on hard substrata. The numerous eggs in each capsule develop over a period of about 2.5 weeks into planktonic veligers. Capsular morphology and hatching time have been documented by BANDEL (1976) who did not, however, describe the stages of embryological development. Here we present data on the deposition of egg masses, embryological development, and the embryonic consumption of capsular "albumen." Although the mode of development and nutrition of embryos are known for some cassids (D'ASARO, 1969; FIORONI, 1966), they have been described in detail only for *Galeodea* (=*Cassidaria*), which is atypical of the family in having relatively few eggs per capsule, embryonic cannibalism, and direct development (FIORONI, 1966; HUGHES, 1986). The genera *Cassis* and *Phalium* (ABBOTT, 1968; D'ASARO, 1969) produce numerous eggs per capsule, similar to *Cypraecassis,* and development is probably always indirect.

MATERIALS AND METHODS

Two mating pairs of *Cypraecassis testiculus* were collected while snorkelling at night off St. Lawrence, Barbados. Extensive searching in this and similar habitats around the island failed to reveal further specimens although two egg masses were found, suggesting that the captured snails had visited the habitat temporarily to spawn. Non-spawning individuals perhaps live farther seaward in the wave-washed zone where their echinoid prey are most abundant. In one pair, the male was 4.3 cm in shell length and the female 5.9 cm, whereas in the other the male was 5.3 cm and the female 6.5 cm. The specimens were kept in a water table containing a 4-cm layer of sand and 18-cm depth of running seawater at 29°C. Since collection, each female had eaten several urchins (*Diadema antillarum* [Philippi] and *Echinometra lucunter* [Linnaeus]) over a period of four days before spawning. Several egg capsules were scraped off the aquarium wall each day and examined beneath a Wild dissecting microscope.

RESULTS

Spawning was initiated by the larger female between 2400 and 2430 h. She deposited capsules on the concrete wall of the aquarium (Figure 1) and one hour later consumed a *Diadema antillarum* before burrowing into the sand. On the next evening she emerged from the sand at 0200 h, deposited egg capsules until dawn (0500 h), and then burrowed into the sand. Spawning and feeding were entirely nocturnal for both females. Capsules were deposited in curved, double rows of 10–17 capsules per arc (Figure 1), secured to the substratum by a jellylike cement forming a

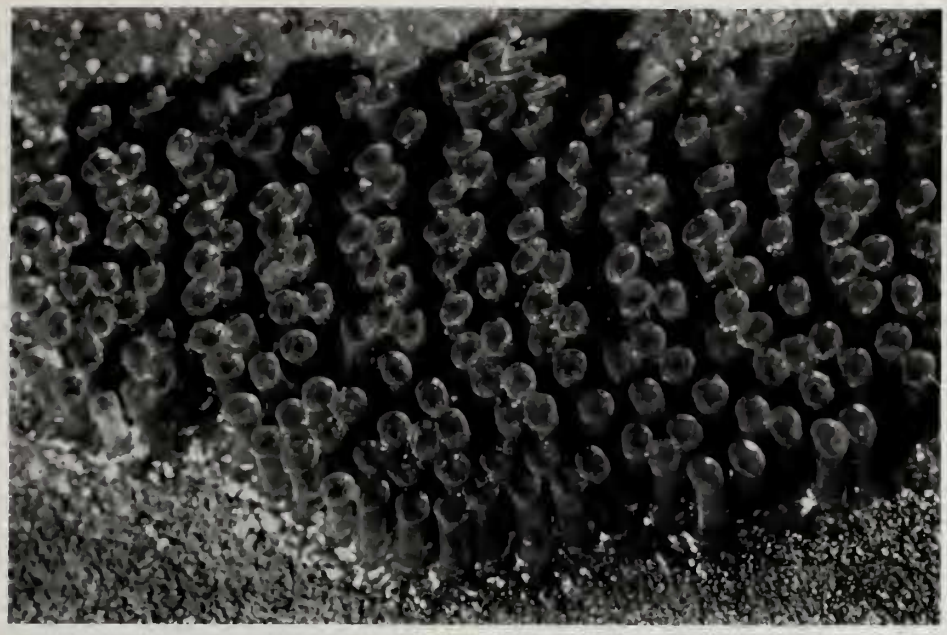

Figure 1

The egg mass of *Cypraecassis testiculus* showing arrangement of the capsules in double arc-shaped rows. Each capsule is about 8 mm tall and 2 mm in diameter. The pigmented eggs impart a deep reddish-purple color to the newly laid egg mass.

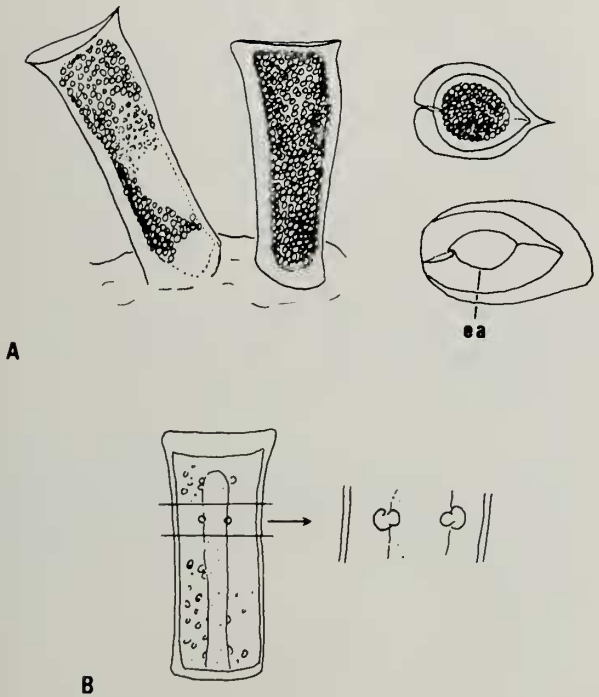

Figure 2

A. The eggs are arranged in a single layer between the capsular wall and a central jelly matrix. The capsular wall is about 900 μm thick. The apical plate of the capsule is elliptical and drawn out into a lateral keel (right hand figures) and is about 2.9 mm in longest diameter. ea, escapement aperture. B. Veligers tend to grasp the central jelly matrix with their velar lobes, as if feeding on it.

common basal sheet for the egg mass. Each capsule was cylindrical with a slightly flared distal rim surrounding the apical plate containing the aperture through which the larvae eventually escaped (Figure 2A). One side of the rim was drawn into a lateral keel, and faint ridges ran along the length of the capsular wall. The eggs formed a single layer, apparently held against the capsular wall by a clear gel (albumen) that filled the lumen.

Development to hatching (Figure 3) took 13–14 days. The deep reddish-purple eggs developed into similarly colored embryos that on the fifth day began to revolve slowly within the spherical egg membrane. By the seventh day, the embryos became more irregular in shape and the egg membrane developed protrusions. By the eighth day, the larvae began to develop the protoconch and the reddish-purple pigmentation became concentrated into two bilateral and one posterior patch. Beating of velar cilia became evident at this stage. By the tenth day, veliger larvae emerged from the egg membranes and were moving freely about the narrow space between the capsular wall and the inner jelly matrix. Macroscopically, the larvae had changed from the initial deep reddish-purple color to

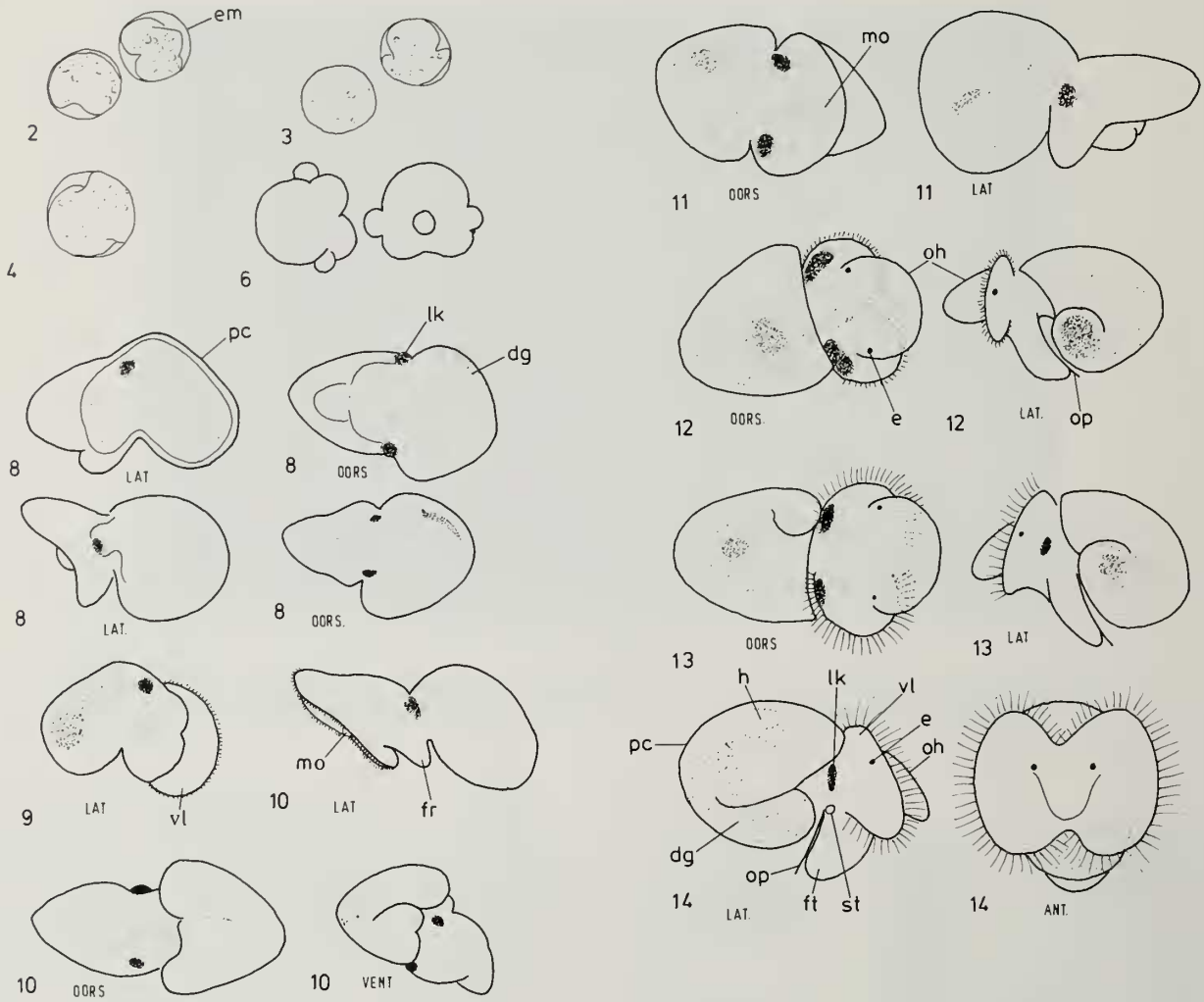

Figure 3

Stages (not all drawn to same scale) in the embryological development of *Cypraecassis testiculus*. Numbers refer to days since oviposition. Approximate sizes of embryos along their major axes are: day 4 = 200 μm, day 9 = 340 μm, day 11 = 400 μm, day 13 = 400 μm. Key: dg, digestive gland; e, eye; em, egg membrane; fr, foot rudiment; ft, foot; h, heart; lk, larval kidney; mo, mouth; oh, oral hood; pc, protoconch; st, statocyst; vl, velar lobe.

a creamy pinkish-brown. By the eleventh day, the protoconch and velum were more fully developed, and some veligers began to grasp the jelly matrix with their velar lobes and appeared to be feeding on it (Figure 2B). This "albumen" matrix shrank considerably during days 10–11, leaving a much wider space between itself and the capsular wall. By the twelfth day, black eye spots and the operculum were visible and the ciliary rim of the velar lobes had become reddish-pink. In many larvae the lateral reddish-brown pigment aggregations had become pinched off into external lobes (larval kidneys) and in some cases these had become detached from the body. By the thirteenth day, many detached pigment aggregations were adhering to the jelly matrix. The colorless heart, the tan-brown visceral mass, and the pair of statocysts in the foot were well developed, and some larvae began to escape from the egg capsules. Most larvae emerged from the capsules within the next 2 days.

DISCUSSION

The deposition of egg capsules in double, arc-shaped rows occurs also in other tonnaceans, notably *Tonna* sp. (Knudson, 1950; Ostergaard, 1950). The general structure of the capsules is similar to that found in other cassids (Abbott, 1968; D'Asaro, 1969; Hughes, 1986) and the arrangement of eggs in a single peripheral layer facilitates

Table 1

Reproductive data for two *Cypraecassis testiculus*.

	Date and number of capsules deposited				
	4/15/ 80	4/16/ 80	4/17/ 80	4/18/ 80	Total
A Spawning schedules					
Large female (6.8 cm)	11	300	400	100	811
Smaller female (5.9 cm)		200	350	250	800
B Measurement of eggs and larvae					
Mean number of eggs per capsule	= 1529, SE = 26, n = 6				
Mean number of eggs per female	= 1.23 × 10^6, n = 2				
Mean diameter of eggs at day 1	= 149 μm, SE = 3, n = 28				
Mean height of protoconch at hatching	= 0.2 mm, SE = 0.01, n = 25				
Number of whorls at hatching	= 1.5				
Mean height of protoconch at apex of adult shell (*i.e.*, at settlement)	= 2.5 mm, SE = 0.2, n = 15				
Number of whorls at settlement	= 3 to 4				

gaseous exchange, as it does in other prosobranchs producing egg capsules (STRATHMANN & CHAFFEE, 1984).

Jettison of the pigmented larval kidneys prior to emergence from the capsule may be a means of disposing of waste products. It has also been recorded in *Crepidula fornicata* (Linnaeus, 1758) (CONKLIN, 1897) but its significance and generality remain to be verified (Rivest, personal communication). Although the larval kidneys excrete granules in *Thais haemastoma floridana* (CONRAD, 1837), they are themselves absorbed by the veligers prior to hatching (D'ASARO, 1966). Other aspects of embryological development in *Cypraecassis testiculus* are typical of related prosobranchs. Cannibalism among sibling veligers was not observed and, since the eggs are not heavily endowed with yolk, planktotrophic development appears likely. Indeed, planktotrophy would be essential to sustain migrants during their transatlantic journey to western Africa (SCHELTEMA, 1978), where a race of *C. testiculus* is also found (ABBOTT, 1968). A prolonged planktonic phase is indicated by the ten-fold increase in height of the protoconch between hatching and initial growth of the teloconch at settlement (Table 1). Larvae of *Cypraecassis testiculus* probably share the planktotrophic habit with *Cassis* spp. (D'ASARO, 1969) but not with the cassid *Galeodea echinophora* (Linnaeus, 1758) in which abortive embryos are cannibalized, allowing development to proceed to the crawling stage prior to emergence from the capsule (HUGHES, 1986). Planktotrophic development in *C. testiculus* is commensurate with a high fecundity, about 1.2 million eggs per female per spawning (Table 1) compared with a fecundity of about 2000 eggs per female per spawning in *G. echinophora*. Whether spawning occurs more than once a year remains unknown.

ACKNOWLEDGMENTS

This research was generously funded by a Royal Society travel grant to R.N.H. We thank Finn Sander for facilities at the Bellairs Research Institute of McGill University at Barbados.

LITERATURE CITED

ABBOTT, R. T. 1968. Helmet shells of the world (Cassidae) 1. Indo-Pacific Mollusca 2:7–201.

BANDEL, K. 1976. Die Gelege Karibischer Vertreter aus den uberfamilien Strombacea, Naticacea und Tonnacea (Mesogastropoda) sowie Beobachtungen im Meer und Aquarium. Mitt. Inst. Colombo-Aleman Invest. Cient. 8:105–139.

CONKLIN, E. G. 1897. The embryology of *Crepidula*, a contribution to the cell lineage and early development of some marine gastropods. J. Morphology 13:1–226.

D'ASARO, C. N. 1966. The egg capsules, embryogenesis, and early organogenesis of a common oyster predator, *Thais haemastoma floridana* (Gastropoda: Prosobranchia). Bull. Mar. Sci. 16:884–914.

D'ASARO, C. N. 1969. The spawn of the emperor helmet shell, *Cassis madagascariensis* Lamarck, from south Florida. Bull. Mar. Sci. 19:905–909.

FIORONI, P. 1966. Zur Morphologie und Embryogenese der Darmtraktes und der transitorischen Organe bei Prosobranchiern (Mollusca, Gastropoda). Rev. Suisse Zool. 73: 621–876.

HUGHES, R. N. 1986. Laboratory observations on the feeding behaviour, reproduction and morphology of *Galeodea echinophora* (Gastropoda: Cassidae). Zool. J. Linn. Soc. 86:355–365.

HUGHES, R. N. & H. P. I. HUGHES. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 29:385–402.

KNUDSEN, J. 1950. Egg capsules and development of gastropods from west Africa. Atlantide Reports 1:85–130. Danish Science Press: Copenhagen.

OSTERGAARD, J. M. 1950. Spawning and development of some Hawaiian marine gastropods. Pacific Sci. 4:75–115.

SCHELTEMA, R. S. 1978. On the relationship between dispersal of pelagic veliger larvae and the evolution of marine prosobranch gastropods. Pp. 303–322. *In:* B. Battaglia & J. A. Beardmore (eds.), Marine organisms: genetics, ecology and evolution. Plenum Press: New York.

STATHMANN, R. R. & C. CHAFFEE. 1984. Constraints on egg masses. II. Effects of spacing, size, and number of eggs on ventilation of masses of embryos in jelly, adherent groups, or in thin-walled capsules. J. Exp. Mar. Biol. Ecol. 84:85–93.